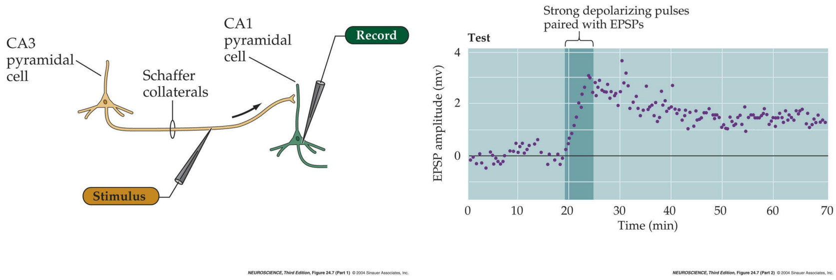

Figure 54: Pairing presynaptic and postsynaptic activity causes LTP.

strongly activated, both synaptic pathways undergo LTP. Note, that this is a cellular analog of the previously discussed mechanism for classical conditioning.

5.7 Hebbian learning

The simplest plasticity rule that follows the spirit of Hebb's conjecture takes the form

$$\tau_w \frac{dw}{dt} = vu - \lambda v \tag{20}$$

where w is the synaptic strength, τ_w is a time constant that controls the rate at which the weights change, and u and v are the neural activity of the pre- and post-synaptic cell, respectively. The first term on the right hand side of Eq. 20 is the Hebbian term and increases the synapses proportional to the product of pre- and post-synaptic activity. Hebbian plasticity is a positive-feedback process because effective synapses are strengthened, making them even more effective. This tends to increase post-synaptic firing rates excessively.

The second term is an effective way of controlling this instability and decreases the synapse proportional to the total post-synaptic activity. λ is an adjustable constant. For one presynaptic neuron and one post-synaptic neuron the net effect is that the synapse is increased (decreased) when the pre-synaptic activity $u > \lambda$ ($u < \lambda$).

When u and v are changing with time, w will also change with time according to Eq. 20. A nice simplification can be made when we assume that

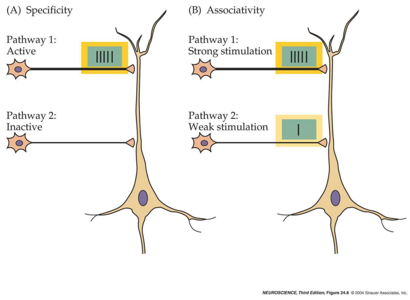

Figure 55: A) Strong activity initiates LTP at active synapses without initiating LTP at nearby inactive synapses. B) Weak stimulation of pathway 2 alone does not trigger LTP. However, when the same weak stimulus to pathway 2 is activated together with strong stimulation of pathway 1, both sets of synapses are strengthened.

u and v are randomly drawn from a probability distribution $p(u,v)$. In this case the average synaptic weight satisfies

$$\tau_w \frac{dw}{dt} = \langle vu \rangle - \lambda \langle v \rangle$$

with $\langle uv \rangle = \int dudvp(u,v)uv$ and $\langle v \rangle = \int dudvp(u,v)v$.

When a neuron receives input from n synapses with strength w_i, the deterministic rule becomes

$$\tau_w \frac{dw_i}{dt} = vu_i - \lambda v, \quad i = 1, \ldots, n \tag{21}$$

Note, that the change of each synapse depends on the value of all other synapses through v. For instance, if we assume that v depends linearly on the inputs $v = \sum_{i=1}^n w_i u_i$.

5.7.1 Ocular dominance

Hebbian plasticity is often used to model the development and activity-dependent modification of neuronal selectivity to various aspects of a sensory input, for example the selectivity of visually responsive neurons to the orientation of a visual image. This typically requires competition between synapses, so that the neuron becomes unresponsive to some features while growing more responsive to others. The above Hebbian rule Eq. 21 introduces such competition, as we will show now.

We consider the highly simplified case of a single layer 4 neuron that receives input from just two LGN neurons with activity $u_i, i = 1, 2$. Two synaptic weights $w_i, i = 1, 2$ describe the synaptic connection strengths of the LGN neurons with the cortical neuron. The output activity we assume simply linear:

$$v = \sum_{i=1}^{2} w_i u_i \tag{22}$$

Thus, Eq. 21 becomes

$$\begin{aligned} \tau_w \frac{dw_i}{dt} &= \sum_j Q_{ij} w_j - \lambda(w_1 \langle u_1 \rangle + w_2 \langle u_2 \rangle) \\ Q_{ij} &= \langle u_i u_j \rangle \end{aligned} \tag{23}$$

Using the symmetry property that both eyes are equal, we can parameterize the matrix as $Q_{11} = Q_{22} = q_s$, $Q_{12} = Q_{21} = q_d$ and $\langle u_1 \rangle = \langle u_2 \rangle = \langle u \rangle$. We can solve Eq. 23 by changing to the basis of eigenvectors of Q. Stated differently, the dynamical equations for $w_1 + w_2$ and $w_1 - w_2$ decouple:

$$\tau_w \frac{d(w_1 + w_2)}{dt} = (q_s + q_d - 2\lambda \langle u \rangle)(w_1 + w_2) \tag{24}$$

$$\tau_w \frac{d(w_1 - w_2)}{dt} = (q_s - q_d)(w_1 - w_2) \tag{25}$$

For λ sufficiently large, the first equation will yield the asymptotic solution $w_1 + w_2 = 0$. Under normal circumstances, the cross correlation between eyes q_d is smaller than the autocorrelation q_s. Therefore, $q_s - q_d > 0$ and $w_1 - w_2$ will grow indefinitely. In reality, there will be non-linearities in the system (in Eq. 20 and Eq. 22) that will prevent this indefinite growth. The final solution is then

$$w_1 = -w_2 = w_\infty \tag{26}$$

with w_∞ a positive or negative value depending on the sign of the initial value $w_1(0) - w_2(0)$. For $w_\infty > 0$, the cortical neuron will be sensitive to eye 1 and insensitive to eye 2, and vise versa. Thus, we have shown that ocular dominance can explained as a consequence of Hebbian learning.